# The prudent parent

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# THE PRUDENT PARENT: ENERGETIC ADJUSTMENTS IN AVIAN BREEDING [1])

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## 1. INTRODUCTION: THE DILEMMA OF THE PRUDENT PARENT

We accept Lack's (1968) contention that features characterizing breeding in birds such as laying date, clutch size, growth rate and duration of the nestling period have all evolved so that in their natural habitat "the birds concerned produce, on average, the greatest possible number of surviving young". Lack identified the main selective pressures responsible as "the availability of food, especially to the young and to a lesser extent to the laying female, and the risk of predation on eggs, young and parents". He closed his book by deploring the circumstantial nature of his evidence (mainly comparisons drawn between closely related species) and urged future workers to engage in field experiments. This approach he considered more valuable than his speculative one, but he warned that experimentation would help to clarify interpretation of breeding adaptations only "if the experimenter is a naturalist capable of designing appropriate experiments and of appreciating the complexity of each situation".

In taking up this challenge we must first explore the context of the question. Implicit in Lack's approach is an emphasis on the pooled wisdom of the species, that is the genetic component, explicable only in terms of the ultimate survival value of the trait. In this view field experiments are expected to demonstrate why the species has arrived at a favoured range of laying dates, clutch sizes, or some other breeding parameter. This can be done by comparing the fates of young born early or late, or originating from broods of various sizes. The difficulty in this approach is that this best of all possible worlds is not met with: most individual birds are cautious parents. The majority of parents delay laying to beyond the most favourable date *i.e.* beyond the date giving maximum probability of nestling survival for the population (Murton 1961, Lack 1966, Perrins 1970, Harris 1969) and produce a clutch smaller than the most productive one (Perrins & Moss 1975; Drent & Ward, in prep.). We are forced to the interpretation that achievement of the most productive laying date and clutch size must entail a substantial decline in subsequent survival were most parents to attempt this. The salient problem is thus that there is not one invariant answer to the question "when should I lay my first egg" or "how many eggs should I lay" but instead the answer appears to depend on some interplay between local environmental conditions and the state of the parent (general proficiency as influenced by experience and state of energy and nutrient balance). Differences between parents and among the same parents from year to year thus become the vital points demanding explanation rather than annoying uncertainties clouding the major issue of species patterns. In our opinion field experimentation aimed at evaluating the adaptedness of breeding patterns should place the question in the framework of individual selection. It should emphasize the adaptive significance of phenotypic variation, the fine adjustment allowing a continuously close fit to altering environmental conditions and equally shaped by natural se-

[1]) dedicated to Prof. dr. Lars von Haartman on the occasion of his 60th birthday.

lection (Lack 1954, Clutton-Brock & Harvey 1979) as is the more abstract level of the "species strategy". It is our conviction that study of the link between reproductive performance of individual parents and their environments will uncover the substrate of decision on which the individual relies, and we see this as the necessary first step towards interpretation of the broad pattern abstracted in the species. Obviously the parent cannot measure increments in death rate as a way of evaluating the options open to it at the time, but the monitoring of energy balance offers possibilities as this may conceivably be closely related to probability of survival.

We thus advocate an approach emphasizing the proximate controls exerted by local food supply on reproductive performance, as an avenue towards understanding the shaping of the breeding pattern of the species by food supply as an ultimate factor defining survival value. The first question to be posed, is if evidence exists that through shortage of some specific nutrient or energy some individual parents fail to lay eggs at all. Secondly, one can ask to what extent energy (or nutrient) shortage imposes a limitation on laying date. Although energy (nutrient) limitation may affect clutch size directly, clutch size is usually considered in relation to the size of the resulting brood. Hence, the third level of limitation concerns the question if the foraging capacity of the parents, itself determined by some interplay between time and energy, in fact sets the upper limit to brood size. A related issue is the role of variation in growth rate in matching demand of the young to parental ability. We will examine the cost of growth, and attempt to estimate the savings on the daily demand incurred by a depressed growth rate.

We emphasize the direct link between the environment (particularly the food supply) and reproductive performance because we are convinced that this influence is pervasive, and not something exceptional to certain highly specialized species as originally envisaged by Lack (1954).

## 2. CONDITION THRESHOLDS FOR BREEDING

The crudest level for the role of food in reproductive performance concerns the bird's decision whether to breed or not. Proof that when feeding conditions are extremely poor, birds will not breed at all, is hard to come by. However, failure to breed in years of rodent scarcity has been indicated in such rodent predators as the Rough-legged Buzzard *Buteo lagopus* (Hagen 1969), the Tawny Owl *Strix aluco* (Southern 1969) and the Barn Owl *Tyto alba* (de Bruijn 1979). The existence of some threshold value of body condition for breeding to be attempted has been hinted at by some recent work on arctic-nesting geese. The critical importance of body reserves in enabling reproduction in wildfowl migrating to the tundra of the arctic to breed, has been realized since Barry (1962) determined the cycle of body weight in the Brent Goose *Branta bernicla* in relation to the breeding cycle. Ryder (1967, 1972) found feeding during laying and incubation highly restricted in the Ross Goose *Chen rossii* and emphasized with weight data that successful breeding was dependent on reserves the female had accumulated before arrival in the arctic. Harvey (1971) suggested that depletion of energy reserves was the major cause of nest desertion by the female Lesser Snowgeese *Chen caerulescens*.

Evidence corroborating the narrow margins intervening between starvation and successful incubation has been presented by Ankney & MacInnes (1978) by detailed carcass analyses for this species. Ankney & MacInnes found that differences in body weight at arrival were reflected in differences in potential clutch size as estimated by follicle development (their data are summarized in Fig. 1).

Given this rigorous regime, reproductive performance should depend on individual condition. The most direct test is to compare reproductive performance with individual body weight obtained at the point of departure from the spring staging areas. Ebbinge and a team of observers cooperating with him have taken this approach with Brent Geese *Branta bernicla* staging in the Netherlands during spring (and nesting in the tundras of coastal Siberia). The programme is to capture birds towards the end of the staging period, to record body weight, and to apply leg rings with an individual inscription discernable at 300 meters. In the fall, when the geese return, a

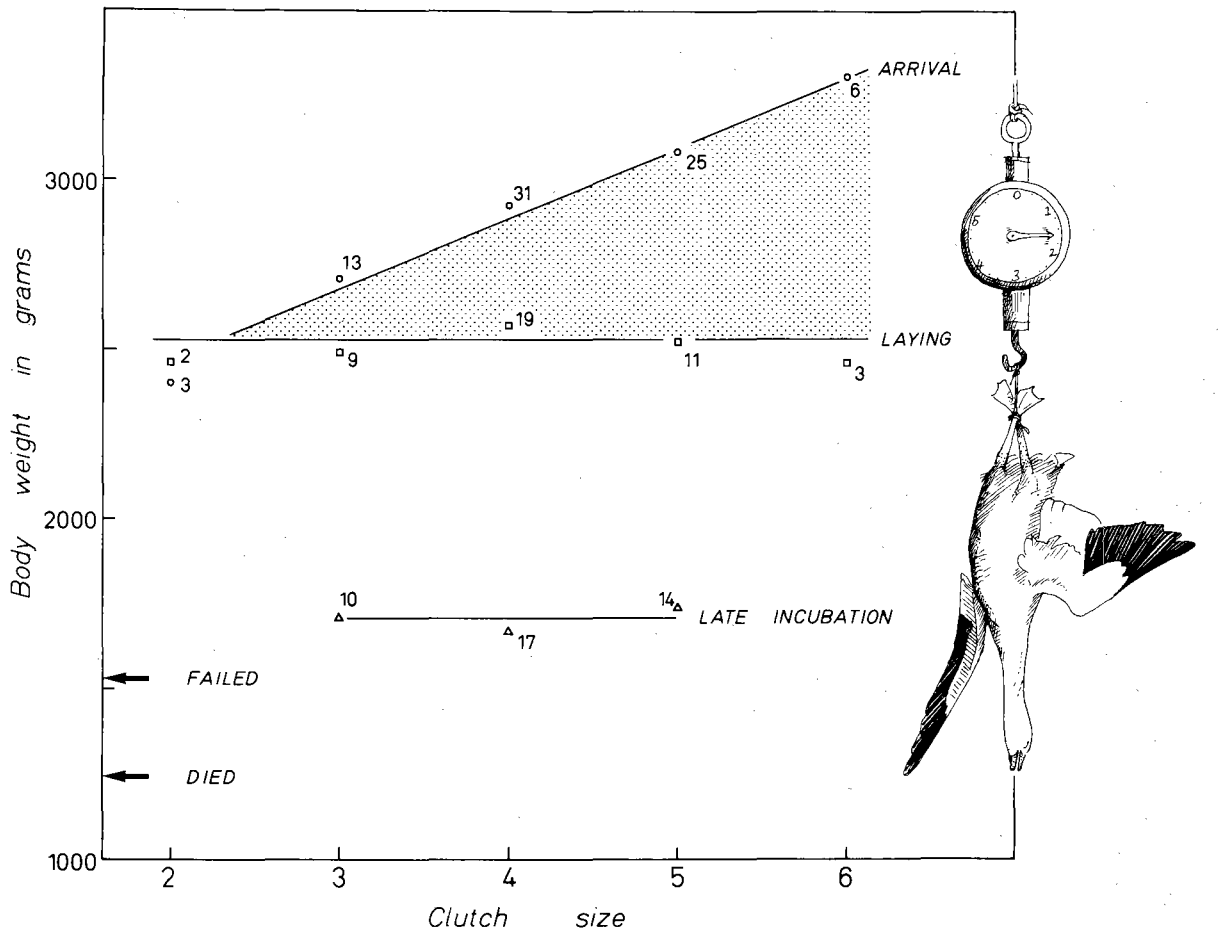


Fig. 1. Change in body weight of female Lesser Snow Geese, *Chen caerulescens*, in the course of breeding in Arctic Canada, in relation to clutch size. Numbers indicate sample sizes of birds collected at the various stages of reproduction. For comparison, mean weights of failed breeders (*i.e.* those abandoning the eggs) and of females dying from starvation on the nest are shown (assembled from data in Ankney & MacInnes 1978).

watch is kept to determine family size for these marked birds (juveniles can be distinguished by plumage characters, and the family behaves as a unit until well into the following spring). Not only was an impressive spread of body weights obtained in these May samples, but these differences are reflected in the probability of returning with juveniles from the actic. Seven females returning with young weighed on average 1618 grams in May (range 1525—1680), whereas eight females returning without young were only 1536 grams in spring (range 1415—1645). This difference is significant ($p < .05$), even though the sample observed is as yet small. In 1976 the sample netted failed to include a single female reaching 1600 grams, and not surprisingly the entire population failed to return with young that year. We do not know whether any eggs were laid that year or if inadequate body condition affected breeding performance after completion of the clutch. A further complication is the influence of environmental factors on the breeding grounds (in particular date of snow melt) which was not measured in this study. However, the results from the goose studies do emphasize the importance of body condition as a predictor of breeding success, and hence its possible use by the bird as a signal to which it may adjust its reproductive commitment.

### 3. LAYING DATE AND CLUTCH SIZE IN RELATION TO FOOD SUPPLY

The physiological drain imposed on the female in forming her clutch has been quantified in only a few species in captivity (King 1973, Ricklefs 1974) but attention has been called to the problem of forming large amounts of protein in a short period of time. Royama (1966a) urged renewed investigation of courtship feeding as a functional transfer of food from the male to his mate during this period of peak demand, and in several species close observation has indeed revealed that the female depends on courtship feeding for a major share of her intake in the period of egg formation (Blue Tit *Parus caeruleus*, Krebs 1970b; Lesser Black-backed Gull *Larus fuscus*, Brown 1967; Common Tern *Sterna hirundo*, Nisbet 1977). Moreover, Nisbet (1973, 1977) was able to show that the rate of provisioning by the male tern influenced female body weight and hence clutch size (and possibly egg size). When Spaans (pers. comm.) increased the rate of courtship feeding in the Herring Gull, *Larus argentatus*, by presenting fish heads to the males on territory, laying was advanced compared to the control pairs, but there was no effect of feeding at this level on clutch size.

Similarly Yom-Tov (1974) was able to advance the laying date of the Crow *Corvus corone* by five days (14 April compared to 19 April for controls) when supplementary food was offered in ten territories, admittedly a subtle effect in view of the early date (1 January) on which the feeding trial started. Källander (1974) advanced the laying date of experienced birds by 3—4 days and of first breeders by 6—7 days in a massive feeding experiment with the Great Tit *Parus major* in Sweden where mealworms were offered in certain blocks of the wood (and the treatment reversed in the second season of the experiment to confirm the role of the food supplement). Inspired by Cavé's (1968) demonstration that timing and degree of development of the ovaries could be influenced by the feeding regime in captive Kestrels *Falco tinnunculus*, we decided to embark on a supplementary feeding experiment in 1978 and 1979. By way of illustration, the main result from this study (Dijkstra *et al.*, in prep.) is summarized in Fig. 2. In the study area, with nestboxes inhabited by circa 20 pairs of Kestrels, some selected pairs were supplied with dead mice (100 g) every other day throughout February, March and the first half of April. This food supplement resulted in clutches which were both considerably earlier (average date of first egg 8 April) and larger (5.6 eggs) than the controls (8 May and 4.6 eggs, respectively in the two seasons of study). The outcome experimentally confirms Cavé's view (1968) that food is causally involved in the combined effects on clutch size and laying date of year-to-year and spatial variations in rodent density. Of the five females obtaining additional food either directly or from their mates, four were caught in the period of one to six weeks prior to laying. All of these turned out to be considerably heavier than other individuals at the same time of year (see fig. 3). From an analysis of body weights of incubating female Kestrels, a close correlation between weight and clutch size was found to exist. Thus, as in the Snow Geese and Nisbet's Common Terns, clutch size appears directly dependent on female condition as reflected by its body weight (the data do not however preclude the possibility that part of this weight variation is not related to short-term condition factors). Since in Kestrels the female discontinues most of her hunting activity shortly

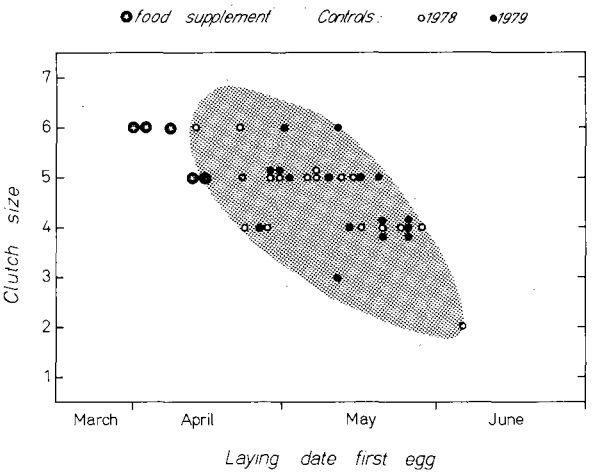


Fig. 2. Effect of supplementary feeding on clutch size and laying date in the Kestrel, *Falco tinnunculus*. Five pairs supplied with mice laid earlier and produced larger clutches than the controls (each symbol indicates events at one nest). Data of Dijkstra *et al.* (in prep.).

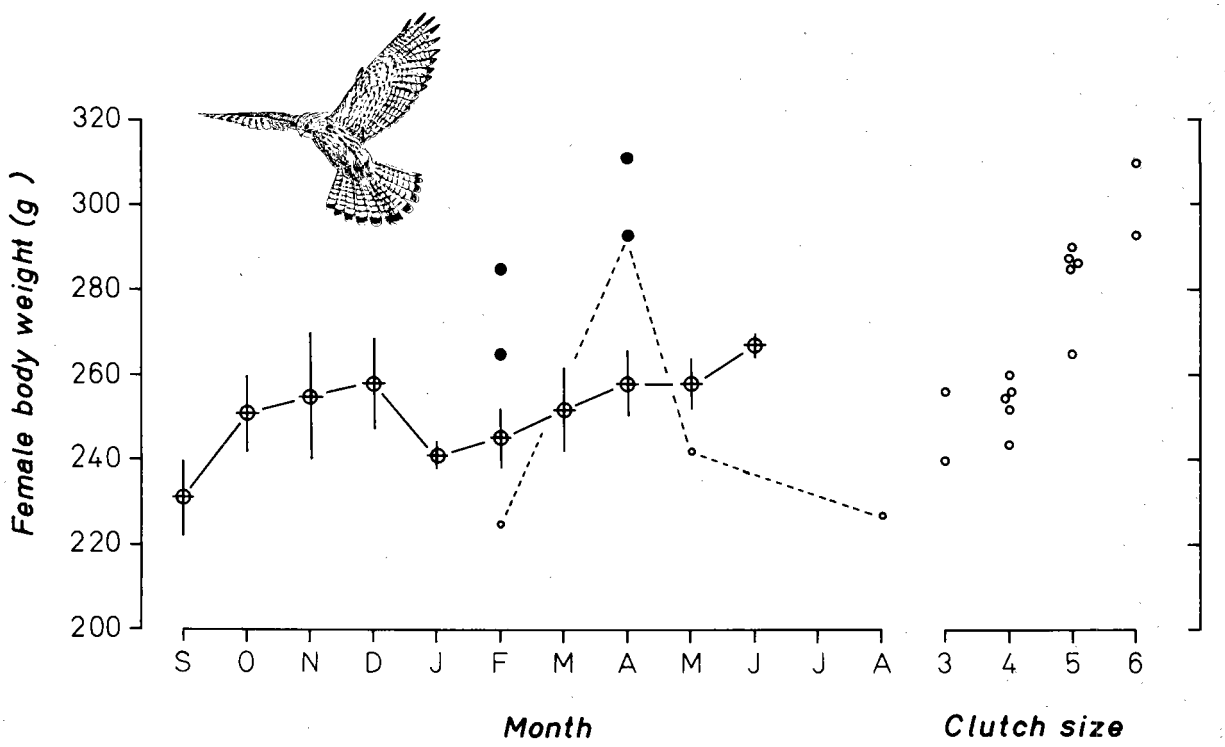


Fig. 3. Body weight in the female Kestrel in the course of the season (left panel, where weights of hens receiving supplementary food are shown by the heavy dots in relation to the controls, where means and standard errors of the means are shown; in one case weights of the hen before and after the food supplement are known, the broken line) and in relation to clutch size (right panel, body weight during early incubation, including the foodsupplemented hens). Data of Daan *et al.* (in prep.), concerning birds caught by balchatri.

before starting her clutch, at this time it is the male who takes most of the credit for her body condition. A direct link between male hunting success, female condition, clutch size and laying date is indicated by the case history of two pairs, closely studied by Masman *et al.* (in prep.) and summarized in Fig. 4. The male of one pair of Kestrels was clearly superior to the male of a neighbouring pair in its rate of prey capture. Independent data on vole densities and comparisons of hunting success indicate that this difference in all likelihood was related to differences in the quality of the hunting area. In any case it contributed to a considerable difference in body weights of the two females, and eventually in their clutch size and laying date.

Thus, a picture emerges that clutch size and laying date, two prime parameters determining reproductive success, are within certain limits directly related to feeding conditions. At least in some species this link has now been experimentally confirmed. Quite apart from its role in differentiating between individual's breeding successes, it may well operate on a population level or on an even wider scale. Several wader species, including the Lapwing *Vanellus vanellus*, have advanced their breeding season by two weeks in The Netherlands in the past half century (Beintema, 1979). A proximate control via enhanced feeding conditions, due to increased fertilizer use in this period, may be the mechanism responsible for this shift. In this species, Högstedt (1974) demonstrated a clear correlation between the time interval from arrival in the breeding area till the onset of laying and the local lumbricid worm stocks.

The physiological mechanism by which food intake affects laying date and clutch size has so far hardly been touched upon here. A significant contribution was made by Jones & Ward (1974)

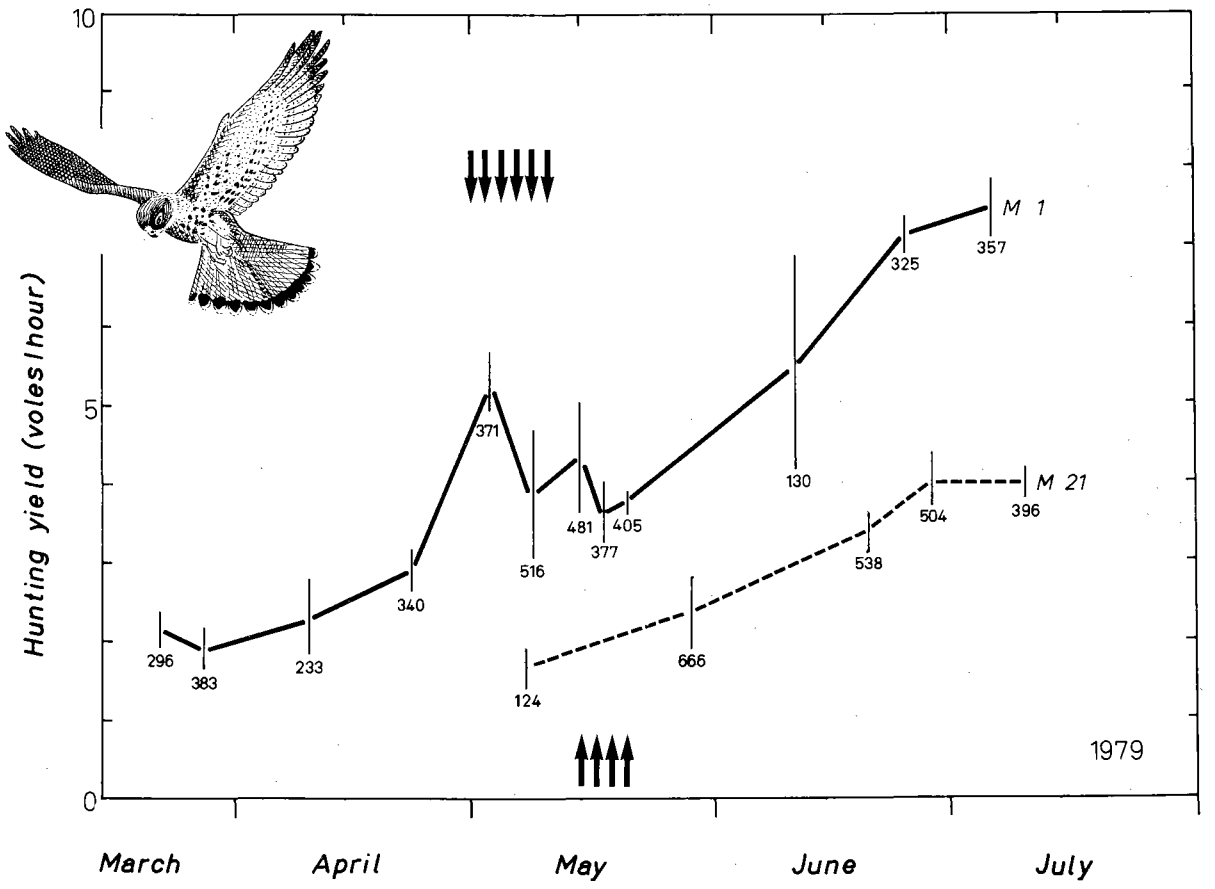


Fig. 4. Hunting success (expressed as voles per hour of flight-hunting) of two male Kestrels with adjacent hunting grounds in relation to season. Vertical lines connect maximum and minimum estimate over two days of observation. Sample sizes are indicated in minutes of flight-hunting observed. The partner of Male 1 commenced laying on 1 May and produced six eggs (see arrows), whereas Male 21's hen delayed starting her clutch of four eggs until 15 May (see text). Data of Masman *et al.* (in prep.).

in the analysis of protein stocks in Weaverbirds *Quelea quelea*. Protein is stored by females of this species in the pre-laying period primarily in the *pectoralis* muscles. The critical finding is that protein values after clutch completion are closely similar for females laying clutches of two, three or four eggs. The rate of protein loss acts as the proximate regulator of clutch size, being dependent on the size of its initial stock as well as on the rate of depletion. The latter depends on the intake rate during laying, *i.e.*, the rate at which the protein store is supplemented from daily food intake. Of course this intake reflects foraging efficiency at the time of laying, which in turn may be of predictive value for rates of intake later on in the season. Thus protein stocks in *Quelea* appear to be involved in the timing of laying as well as in the size of the clutch produced.

Up to this point we have considered the start of laying each season, but a related problem is posed when second broods are undertaken. Kluyver and his colleagues (Kluyver *et al.* 1977) have recently taken a fresh look at this problem in the Great Tit. For the suboptimal pinewoods habitat (Hoge Veluwe study area) a nine-year run of data on food supply (as measured from caterpillar frass caught on trays) and the mean interval between first and second broods showed that this interval was shorter in years of rich food supply, suggesting that when the females were in a position to recover condition quickly they

could start a new brood without delay. Further support for this conclusion was provided by the demonstration that the interbrood interval was shorter the fewer young had been raised in the first breeding attempt (thirteen years' data for Hoge Veluwe as well as congruent findings from the experiments on Vlieland where in certain years many broods were reduced leading to shorter interbrood intervals). In deciduous woods, where the data were more limited, these effects were not shown with statistical reliability. Turning next to a consideration of the incidence of second broods, the authors were unable to reconcile the finding that second broods were undertaken far less frequently in deciduous woods than pinewoods, even though absolute food levels are still much higher in the former at that time (van Balen 1973) and they abandoned the food-condition link as an adequate explanation, proposing instead some direct effect of breeding density (inversely related to the incidence of second broods). The more general interpretation, that the incidence of second broods is determined by the condition of the female, dependent in turn on food supply as mediated by total bird density in the habitat, can nevertheless be advanced here too, as we will show. Kluyver *et al.* (1977) re-analysed the data on local survival of young tits ringed as nestlings in the study areas Liesbosch (optimal habitat) and Hoge Veluwe (marginal habitat) in the years 1955—1966. Originally grouped by calendar date, (Kluyver 1971) the data were now (Kluyver *et al.*, table 14) subdivided into five-day periods starting from the earliest clutch of each season. We must bear in mind that the level of returns may not be a completely reliable indication of the absolute recruitment because of differences between the two study areas in the level of emigration. The shape of the curve (Figure 5) for each area does however allow speculation as follows. Feeding conditions, as assayed by the subsequent fate of birds fledged, remain favourable for a much longer period in the marginal habitat, and can indeed be considered still good at about the time second broods must be started. Differences in the intensity of intra-specific competition may prove a more directly related parameter (it will be recalled that density in the pinewoods at that time

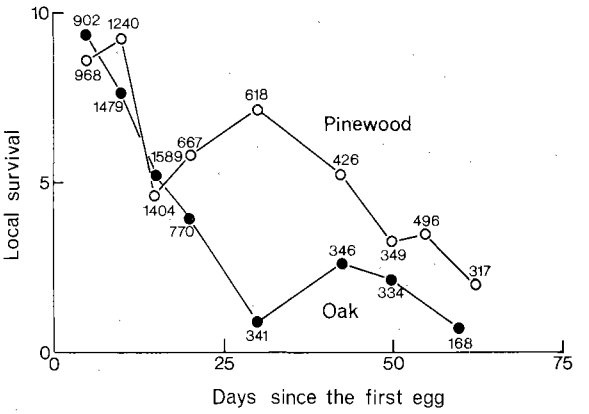


Fig. 5. Local survival of Great Tit fledglings (return in area of origin) in relation to laying date and habitat. Survival from clutches commenced more than two weeks after the first egg of the season is consistently higher in the pinewood Hoge Veluwe than in the oakwood Liesbosch. Sample sizes are the number of young ringed in the years 1955—1966 (assembled from Kluijver *et al.* 1977). Perspectives for second broods are thus less favourable in deciduous woods than in the low density pinewood habitat.

is far lower), but we feel that direct study of condition of individual birds should be undertaken to investigate the avenue of proximate control of initiation of the second brood.

The problem of the proximate control of the decision to commence a second (or subsequent) clutch can only be solved when the energy balance and current state of the body reserves can be followed in individual birds. The perspectives for such work are promising: thus Hails & Bryant (1979) have evidence from determination of energy expenditure of individual House Martins *Delichon urbica* that the energy cost of collecting food for the nestlings was higher in the period of second broods than earlier in the season, and they speculate that this increased cost may be related to a qualitative change in the insect prey spectrum brought to the nest. This example shows that measurement of individual energy budgets is now possible for free-living birds by utilizing the doubly-labelled water $D_2O^{18}$) technique, and, secondly the findings on the House Martins are in accord with the view of proximate control of reproductive effort developed from the work on Kestrels and Great Tits.

Before leaving this section on problems of

laying date and clutch size we shall attempt to clarify our concept of how proximate and ultimate factors intertwine by providing two diagrams (Fig. 6a and 6b). The fact we seek to interpret is the seasonal decline in clutch size found in so many birds, keeping in mind the dependence of laying date and clutch size on body condition as revealed by the supplementary food experiments. In ultimate terms, the adaptive value of the seasonal decline in clutch size depends on the decline in returns, *i.e.* survival probability of the nestlings, as the season progresses (see Fig. 6a). There is a great deal of evidence in a variety of species that young born late are at a serious disadvantage (see *e.g.*, Fig. 5), and we take the food supplement experiments to mean that the individuals concerned would lay earlier if their condition allowed them to. The penalty of delay in laying and its relation to the optimal choice of clutch-size must somehow be related to female body condition which will tend to improve with time (as protein and other reserves are stored in the body).

Let us reduce the female's problem of determining clutch size to her decision to make one extra egg or not. When she has reached a condition sufficient to lay $x$ eggs, the curves for the number of offspring surviving from clutches with size $x$ and size $x + 1$ will ultimately determine whether she should delay egg-laying until she has attained the condition needed to produce a clutch one egg larger. In our graphic model, the survival probability of the additional egg drops as steeply as that for the other eggs. Hence as the season progresses it becomes less and less worthwhile to wait until enough protein and other body reserves have been accumulated for making the extra egg. The trade-off between a delay in laying in exchange for a larger clutch is thus not fixed but changes in the course of the season. The profits margin of the larger clutch is further eroded by the fact that birds which have to face this decision late in the season are likely to be those who are slow in putting on body condition, and thus would need extra time to prepare for the extra egg. A "high quality" female, with a rapid increase in condition, will leave more progeny if she carries on a short time longer until reaching the level requisite to make the additional egg. A "low quality" female on the other hand will leave more progeny if she sets her target at the smaller clutch: the additional egg with its reduced chance of survival does not compensate for the decline in survival potential suffered by the basal clutch if the female were to incur the delay required to produce the extra egg. Thus some individuals in the population (late arrivals, or perhaps in addition to this disadvantage those relegated to poor habitats, with inexperienced mates etc.) will decide on a small clutch as their own optimal strategy, even though the population optimum may be much larger.

How is this optimal schedule translated into decisions by individual females? Of course we do not imply that the female bird actually estimates the curves of offspring yield (Fig. 6a) to which her strategy is adaptive. In order to reach the optimal solution to her problem she may in principle use either her body condition relative to a changing threshold, or its rate of change relative to fixed thresholds. The first approach would amount to a change in the threshold of condition with the season as part of the circannual machinery of the bird, in essence the model proposed by Reynolds (1972) for the Mute Swan *Cygnus olor*. Crossing the threshold in this model would simultaneously induce laying and determine (by the condition reached) the clutch size. In the alternative model, a bird steeply crossing the condition threshold for laying $x$ eggs responds with continuing till the threshold for $x + 1$ eggs and thus takes the option of an extra egg instead of earlier laying. The poor quality bird, crossing the threshold slowly, would not further postpone laying and be content with a smaller clutch. The two approaches to decision making (Fig. 6b) would be strictly comparable to economic decisions in terms of investment based either on capital available or on the rate of accumulation of capital, *i.e.* current net daily income. The alternatives would clearly produce about the same general result for the population. It may well be, however, that different bird species have indeed evolved different approaches to the same problem. No data seem to be available today to distinguish between "capital based investment" and "income based investment". A critical experimental test would be to assess if clutch size

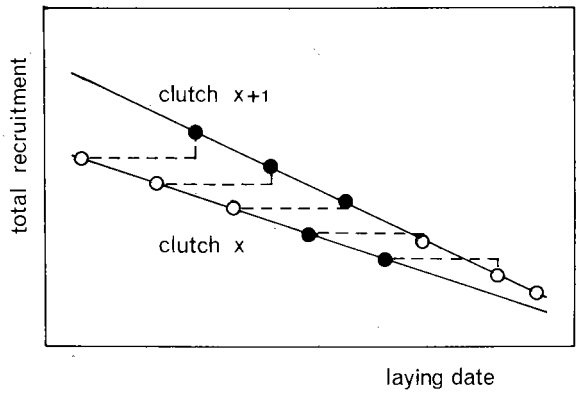


Fig. 6a. Ultimate value of the decision to enlarge the clutch by one egg (optimal clutch size: solid dots). The contribution of the extra egg to total recruitment decreases with laying date. If waiting time (to reach condition sufficient for clutch x + 1) is constant, early parents should wait and lay x + 1, late parents should lay x eggs.

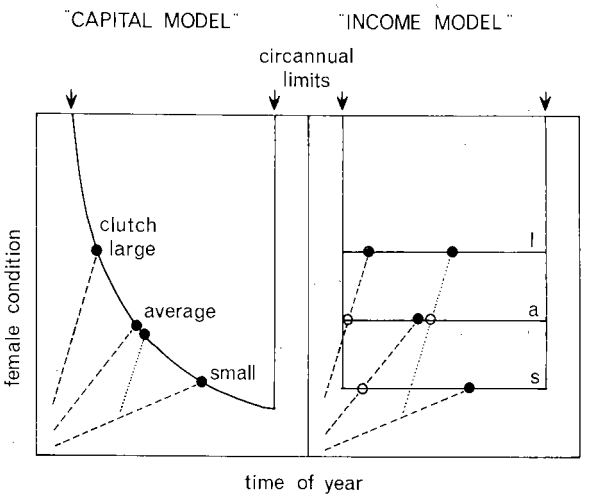


Fig. 6b. Proximate regulation of laying date and clutch size in relation to female body condition: investment models according to a capital or income evaluation (see text) for proximate control to provide decisions adapted to ultimate optimalisation of recruitment. Broken lines: trend lines for body condition in females of varying quality. Dotted lines: predicted change in body conditions of poor birds fed late in the season, resulting in the predicted clutch sizes: average in the "capital" model, large in the "income" model.

can be increased independently of laying date by supplementary feeding. This test can be done in birds with a large variation in laying date (such as, for instance, Kestrel, Barn Owl or Mute Swan) by providing the late layers of the season with additional food, once the first large clutches of the season have been laid already. In the comparison of fed and non-fed birds laying at the same date, the "capital" model predicts no difference, while the "income" model predicts larger clutches in the fed birds (dotted lines in Fig. 6b). Obviously, the possibility of a mixed strategy, exploiting information from both capital (body condition) and income (net daily available energy, or increase in body condition) should not be excluded.

## 4. ENERGETIC IMPLICATIONS OF VARIATION IN GROWTH RATE

Lack championed the view that parents work to capacity and that broodsize and growth rate were adjusted accordingly, "growth requires energy and its rate thus affects the number of offspring that can be raised by birds that feed their young" (Lack, 1968). Support for these ideas was based on consideration of nestling periods (as an indirect measure of growth rate) in relation to clutch size and foraging ecology. Ricklefs (1968, 1973, 1976) has undertaken a more direct analysis of variation in growth rate by applying curve-fitting techniques to growth curves for body weight. Ricklefs emphasized that the characteristic growth rates of species are related to adult body weight, heavier species showing slower rates of development. He found that the single most decisive growth parameter, when this dependence was taken into account, was the age at which flight is achieved, species achieving flight early having depressed rates of growth. Within the nidicolous mode for which Lack advanced his hypothesis on the adjustability of growth rate, Ricklefs was able to confirm Lack's contention that sea-birds with reduced brood-sizes indeed showed reduced growth (Ricklefs 1973). Tropical land birds, especially those that feed fruit of low protein content to their young, also showed reduced growth rates (Ricklefs 1976). That energetic (or nutrient) limitation is indeed concerned, follows from the premise that species should always maximise growth rate to achieve early nest departure, especially where nestling predation is heavy such as it is in the tropics.

Although Ricklefs agreed with Lack's contention that growth was slow in oceanic birds with single egg clutches, he did not consider the issue of the adaptive significance of this flexili-

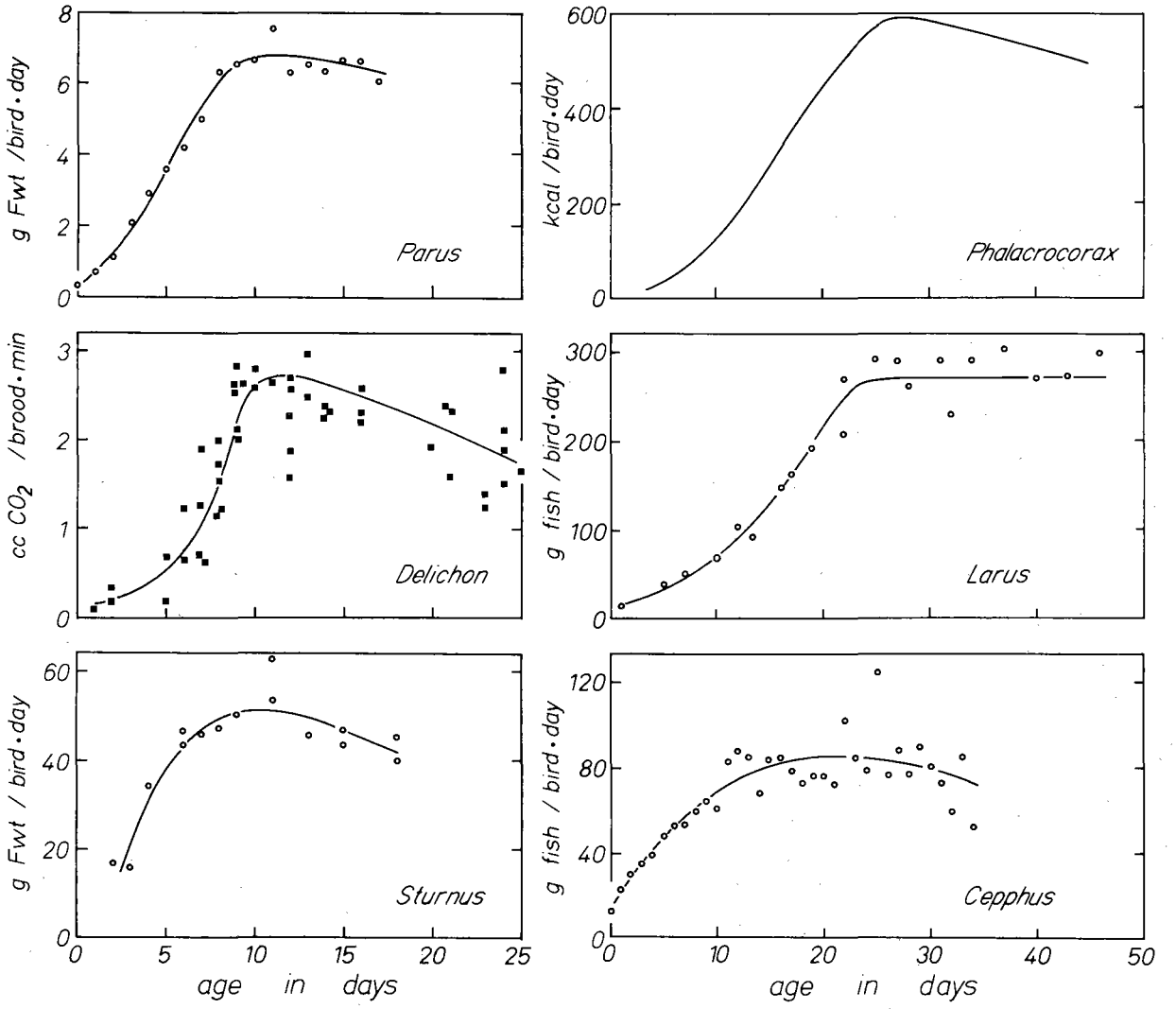


Fig. 7. Rate of food provisioning of nestlings in six species: *Parus major* (van Balen 1973) and *Phalacrocorax auritus* (Dunn 1975) from visual estimates of prey or meal size, *Delichon urbica* (Bryant & Gardiner 1979) where metabolism of a brood of four as measured in the original nest in the field mirrors demand, *Larus glaucescens* (Henderson & Drent, in prep.) where food requirement of captive birds is shown, and finally *Sturnus vulgaris* (Westerterp, in prep.) and *Cepphus columba* (Koelink 1972) where food delivered was weighed by inserting a balance in the nest. In all species demand is already at a peak midway through the nestling period.

bility of growth rate solved, since an algebraic approach to growth cost (Ricklefs 1969, 1974, 1976) indicated that even large changes in daily growth rate would scarcely affect daily energy input. Before examining Ricklefs' growth model, we will demonstrate the flexibility of growth rate in sea-birds in a slightly different way.

We have chosen the absolute growth rate (defined as grams fresh weight per day) taken from the linear period of growth characteristic for birds midway in their development (and virtually identical to the most rapid absolute growth rate selected by Hussell, 1972 in his analysis) in preference to the K-parameter relied on by Ricklefs, because absolute growth rate, unlike K, can be directly converted to cost, and nestling demand peaks at about the time this growth rate is achieved in those species where food intake has been measured (see Fig. 7 where data for six species are assembled). We have selected adult

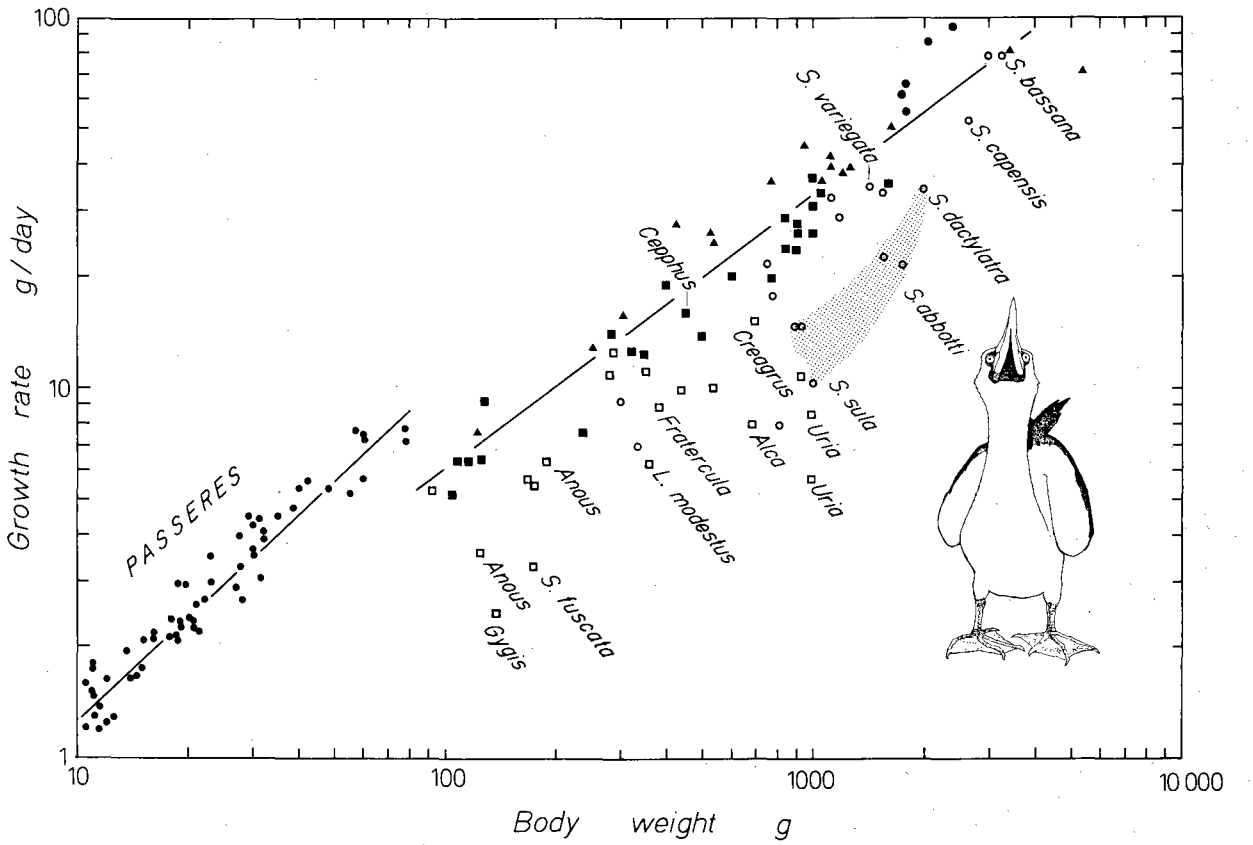


Fig. 8. Absolute growth rate (g fresh weight per day) during linear growth midway through development in relation to adult body weight in pelecaniform (circles), charadriiform (squares) and falconiform (triangles) birds of the nidicolous type (for species see Table 1 and appendix). Solid symbols indicate species with more than one egg per clutch, open symbols such with reduced broods (1 egg; 2 in *Larus modestus*). Pantropical boobies enclosed by stippling. Line indicates linear regression for non-reduced brood sizes. The exponent relating growth rate to mature body size is 0.74. For comparison, data for passerines are included (small dots; computed from Ricklefs 1968, 1973, 1976).

body weight rather than nestling asymptote as point of reference, mainly because nestling asymptote is poorly defined in many of the original studies and hence its level is often a matter of subjective estimate. Moreover the overshoot found in many nestlings is primarily a matter of fat deposition (Bryant & Gardiner 1979) occurring beyond the period of linear or maximal growth covered in our analysis.

When absolute growth rate is compared to adult body weight in nidicolous pelecaniform and charadriiform birds (Table 1, Fig. 8) depressed growth rates are seen to go hand in hand with reductions in the brood-size in specialized species, most of them tropical. In pelecaniform birds, for example, the pantropical boobies stand out as a group with stunted growth rates in comparison to related birds of similar body weight, a point already made by Nelson (summary in Nelson 1978). None of the boobies enclosed by the stippled zone in the figure has been observed to raise more than one young, although several lay more than one egg in which case the supernumerary eggs have been viewed as a form of insurance against egg breakage or infertility. In sharp contrast, the Peruvian Booby, *Sula variegata*, experiencing a richer and more predictable food supply, is often able to raise 2—3 chicks and reaches the growth rate expected of its adult body weight. Frigate birds, with their singleton chicks also show sharply reduced growth rates. Among the auks, the majority of species lay but one egg and show reduced growth rates, the exceptional Pigeon Guillemot *Cepphus columba* with

Table 1 Growth rate in certain sea-birds (Pelecaniformes and Charadriiformes) where the young are fed by the parents (altricial and semi-precocial types)

| | Adult body weight (g) | Daily increase (g) | Locality | Authority |
|---|---|---|---|---|
| *Phaethontidae* | | | | |
| *Phaethon lepturus | 300 | 9.3 | Ascension | Stonehouse 1962, 1963 |
| *Phaethon lepturus | 334 | 7 | Aldabra | Diamond 1975a |
| *Phaethon aethureus | 750 | 22 | Ascension | Stonehouse 1962, 1963 |
| *Phaethon rubricauda | 762 | 12—24 | Aldabra | Diamond 1975a |
| *Pelecanidae* | | | | |
| Pelecanus rufescens | 5150 | 132 | Uganda | Din & Eltringham 1974 |
| *Sulidae* | | | | |
| *Sula sula | 905 | 14.9 | Christmas I. | Nelson 1978 |
| *Sula sula | 912 | 14.9 | Aldabra | Diamond 1974 |
| *Sula sula | 1003 | 10.4 | Galapagos | Nelson 1978 |
| *Sula leucogaster | 1111 | 32.5 | Christmas I. | Nelson 1978 |
| *Sula leucogaster | 1175 | 29.0 | Ascension | Dorward 1962 |
| *Sula variegata | 1410 | 35.0 | Peru | Nelson 1978 |
| *Sula nebouxi | 1542 | 33.9 | Galapagos | Nelson 1978 |
| *Sula abbotti | 1550 | 22.6 | Christmas | Nelson 1978 |
| *Sula dactylatra | 1300 | 34.5 | Ascension | Dorward 1962 |
| *Sula dactylatra | 1754 | 21.7 | Galapagos | Nelson 1978 |
| *Sula dactylatra | 1988 | 34.5 | Kure | Kepler in Nelson 1978 |
| *Sula capensis | 2640 | 52.5 | S. Africa | Jarvis 1974 |
| *Sula bassana | 3000 | 79 | Scotland | Nelson 1978 |
| *Sula bassana | 3220 | 79 | Quebec | Poulin in Nelson 1978 |
| *Phalacrocoracidae* | | | | |
| Phalacrocorax pelagicus | 1750 | 61.6 | Brit. Col. | Robertson 1971 |
| Phalacrocorax aristotelis | 1780 | 66.7 | England | Snow 1960 |
| Phalacrocorax aristotelis | 1785 | 55.5 | England | Pearson 1968 |
| Phalacrocorax auritus | 2047 | 84 | Maine | Dunn 1975 |
| Phalacrocorax auritus | 2400 | 95.9 | Brit. Col. | Robertson 1971 |
| *Fregatidae* | | | | |
| *Fregata ariel | 806 | 8.0 | Aldabra | Diamond 1975b |
| *Fregata aquila | 1250 | 16 | Ascension | Stonehouse & Stonehouse 1963 |
| *Fregata minor | 1314 | 18.8 | Aldabra | Diamond 1975b |
| *Stercorariidae* | | | | |
| Stercorarius longicaudus | 309 | 12.6 | Sweden | Andersson 1976 |
| *Laridae* | | | | |
| Sterna paradisaea | 104 | 5.2 | England | Pearson 1968 |
| Sterna dougallii | 108 | 6.5 | New York | LeCroy & Collins 1972 |
| Sterna hirundo | 116 | 6.5 | New York | LeCroy & Collins 1972 |
| Sterna hirundo | 125 | 6.4 | England | Pearson 1968 |
| Sterna hirundo | 128 | 9.3 | Poland | Szulc-Olechowa 1964 |
| *Anous tenuirostris | 126 | 3.0—4.5 | Ascension | Ashmole 1962 |
| *Gygis alba | 138 | 2.5 | Ascension | Dorward 1963 |
| *Sterna fuscata | 175 | 2.5—4.5 | Ascension | Ashmole 1963, Stonehouse 1963 |
| *Anous stolidus | 186 | 7.5 | Ascension | Dorward & Ashmole 1963 |
| Sterna sanvicensis | 237 | 7.6 | England | Pearson 1968 |
| Larus ridibundus | 285 | 14.3 | Poland | Szulc-Olechowa 1964 |
| Rissa tridactyla | 350 | 11.1 | England | Pearson 1968 |
| *Larus modestus | 370 | 6.4 | Chile | Howell et al., 1974 |
| Larus canus | 400 | 19 | Barents Sea | Belopolskii in Ricklefs 1973 |
| Larus delawarensis | 497 | 13.9 | Alberta | Vermeer 1970 |
| *Larus californicus | 609 | 20.4 | Wyoming | Smith & Diem 1972 |
| Larus californicus | 769 | 20.0 | Alberta | Vermeer 1970 |
| *Creagrus furcatus | 693 | 15.3 | Galapagos | Harris 1970 |

| | Adult body weight (g) | Daily increase (g) | Locality | Authority |
|---|---|---|---|---|
| Larus dominicanus | 890 | 23.3 | New Zealand | Fordham 1964 |
| Larus fuscus | 830 | 29.0 | England | Harris 1964 |
| Larus fuscus | 854 | 23.6 | England | Pearson 1968 |
| Larus occidentalis | 900 | 26 | California | Coulter 1973 |
| Larus argentatus | 895 | 27 | England | Harris 1964 |
| Larus argentatus | 1000 | 30.6 | Netherlands | Spaans 1971 |
| Larus glaucescens | 1050 | 26.3—36.5 | Brit. Col. | Ward 1973 |
| Larus marinus | 1600 | 34.3 | England | Harris 1964 |
| *Alcidae* | | | | |
| *Aethia pusilla | 92 | 5.3 | Alaska | Sealey 1973 |
| *Ptychoramphus aleuticus | 167 | 5.7 | California | Thoresen in Sealey 1973 |
| *Ptychoramphus aleuticus | 162 | 5.3 | California | Manuwal 1979 |
| *Cyclorhynchus psittacula | 280 | 10.9 | Alaska | Sealey 1973 |
| *Aethia cristatella | 286 | 12.5 | Alaska | Sealey 1973 |
| *Fratercula arctica | 380 | 8.9 | England | Pearson 1968 |
| *Fratercula arctica | 440 | 10.0 | Norway | Myrberget 1962 |
| Cepphus columba | 474 | 16.0 | Washington | Thoresen & Booth 1958 |
| Cepphus columba | 450 | 16.5 | Brit. Col. | Drent 1965 |
| *Cerorhinca monocerata | 518 | 10.1 | Brit. Col. | Summers & Drent 1979 |
| *Alca torda | 686 | 8.0 | Quebec | Bédard 1969 |
| *Uria aalge | 925 | 10.8 | England | Pearson 1968 |
| *Uria aalge | 957 | 5.7 | Alaska | Johnson & West 1975 |
| *Uria lomvia | 989 | 8.5 | Alaska | Johnson & West 1975 |

* denotes species with reduced brood size: 1 egg (2 in *Larus modestus*). Excluding species with reduced brood size Table 1 and the appendix (p. 252) provide 48 studies of growth rate in relation to adult body weight in non-passerines. The formula $Y = 0.202. X^{0.74}$ relates Y = daily increase (in g) to X = adult body weight (in g).

its two egg clutch reaching the growth level predicted for its body weight and confirming the applicability of this approach. In the case of *Uria* and *Alca*, more than simply a reduced growth rate is involved, as these genera exemplify a unique developmental mode whereby the young leave the nesting colony only partway through development, and are accompanied to sea by one of the parents who continues to care for them following colony departure. Slow growth is in these species partly explained by a higher priority in feather development compared to the classical nidiculous mode of development shown by the puffins and *Cepphus*. Turning now to gulls and terns, we again see marked growth depression in tropical forms, most of them with but a single egg (*Sterna fuscata*, *Gygis alba*, *Anous tenuirostris*, *Anous stolidus* among the terns). The Swallow-tailed Gull *Creagrus furcata*, although it lays but a single egg, does not show a clearcut growth depression but this species is able to raise twins as Harris (1970) demonstrated experimentally. This is an interesting parallel to the difference in chick-raising ability in the gannets, *Sula bassana* studied by Nelson at the Bass Rock was able to raise artificial twin sets, and indeed the growth rate for this species lies at the expected level. The related *Sula capensis* studied by Jarvis (1974) in South Africa failed to raise twins to adequate fledging weight and indeed normal growth in this species is below the level expected for its body size, indicating an adaptation to feeding conditions more exacting than those experienced by *S. bassana*. The only gull showing clearcut growth depression is the highly specialised *Larus modestus* studied by Howell *et al.* (1974) in the deserts of Chile. This gull lays two eggs and has a bipartite brood patch as contrasted to the three egg clutch characteristic for *Larus* gulls with their three discrete brood patches.

Growth rate has some maximum set by physiological constraints, but the ecological question is if growth rate can be reduced when the daily cost cannot be met by the parent. In the view that reproductive effort is adjusted to parental foraging capacity, brood size is the primary adjustment, and growth rate need only be depressed in species with small families where the integer

steps of adjusting brood-size become too crude (Ricklefs 1968). Studies on procellariiform seabirds cannot assist us here, since the brood-size is invariably one, but in other sea-bird groups with variable family size, our analysis is in full accord with these principles: growth rate is demonstrably highly variable in species with small broods when compared to their close relatives. Some species apparently achieve the physiological maximum dictated by body weight, but the majority show slowed growth as one of the adaptations allowing reproduction in a highly hostile environment (further discussions in Lack (1967, 1968) and Nelson (1978)).

Having established the adjustability of *growth rate*, the next problem is to attempt estimation of the repercussions of these variations for the daily energy intake of the nestlings. Our approach to this problem has been to examine daily energy expenditure in nidicolous birds in relation to growth rate. Available to us were measurements of energy expenditure in kcal per bird per day (here abbreviated as DME or Daily Metabolizable Energy) for eight nidicolous species: *Passer domesticus* (Blem 1975), *Lanius collurio* (Diehl & Myrcha 1973), *Sturnus vulgaris* (Westerterp 1973), *Asio otus* (Wijnandts, in prep.), *Cepphus columba* (Koelink 1972), *Larus glaucescens* (Drent & Henderson in prep.), *Eudocimus albus* (Kushlan 1977) and *Phalacrocorax auritus* (Dunn 1975a, 1975b).

In most cases energy expenditure (DME) has been estimated indirectly by measuring total food consumption (GEI or gross energetic intake) and determining metabolizable energy in digestibility trials where the caloric content of incoming food and outgoing excretory products are measured (ME = GEI - FU where FU = faeces + uric acid). Data for *Sturnus*, *Asio*, *Cepphus* and *Phalacrocorax* rely on weights (or in the case of *Phalacrocorax* visual estimates of volumes) of meals delivered to the nest to arrive at energy income, whereas the data for *Eudocimus* and *Larus* derive from known meal size for young raised in captivity at growth rates comparable to those achieved in wild birds. For *Passer* and *Lanius* the data are derived from measurements of the gaseous metabolism of the entire brood, and in *Lanius* this has been checked against food consumption as determined by measuring meal size with neck collars and counting feeding frequency at undisturbed nests. When these figures are entered against the body weight for the individual nestling concerned (Fig. 9) an overall pattern emerges. Kendeigh *et al.* (1977), who recently made a similar compilation, included both altricial and precocial birds, resulting in greater scatter as energy expenditure in precocial birds is higher at comparable body weight.

The message conveyed by Fig. 9 is that the energy expenditure of birds while in the nest is broadly similar at a given body weight, regardless of whether we are dealing with a songbird, owl, auk, stork, gull, or cormorant. How do these DME values relate to growth rates, or more specifically, are differences in total daily energy expenditure related to differences in absolute growth rate? To answer this question, we determined the absolute growth rate in the linear growth period for the species concerned, and for the interspecies comparison selected the DME at inflection of the growth rate (the midpoint of the linear period of growth) and compared this DME between the species at that point (see Fig. 10). In practice, this is equivalent to taking maximal absolute growth rate and comparing energy expenditure at that point between the species. The points so determined fall along a line with slope indicating the equivalence of 1 g increment in growth per day to the ME value of 5.8 kcal. This figure is roughly in agreement with less complete data for two other nidicolous birds for which energy intake for growth has been measured in captives (6.3 kcal/g weight increment in *Larus canus*, Kahru in prep., 6.9 kcal/g in *Mycteria americana*, Kahl 1964). Perhaps more surprisingly, it is also in accord with the caloric equivalent of body weight changes in adult birds deduced from energy balance trials (Dolnik & Gavrilow 1971; Cain 1976; Owen 1970; Kendeigh *et al.* 1977). It would be incorrect to conclude that 5.8 kcal are required to build one g of body mass, all that we can say is that a difference in rate of growth of 1 g is associated with this total cost. Part of this requirement represents the cost of biosynthesis and the remainder the cost of maintenance (probably in the neighbourhood of 2.5—3.5 kcal/g judging from energy expenditure of nestlings in periods

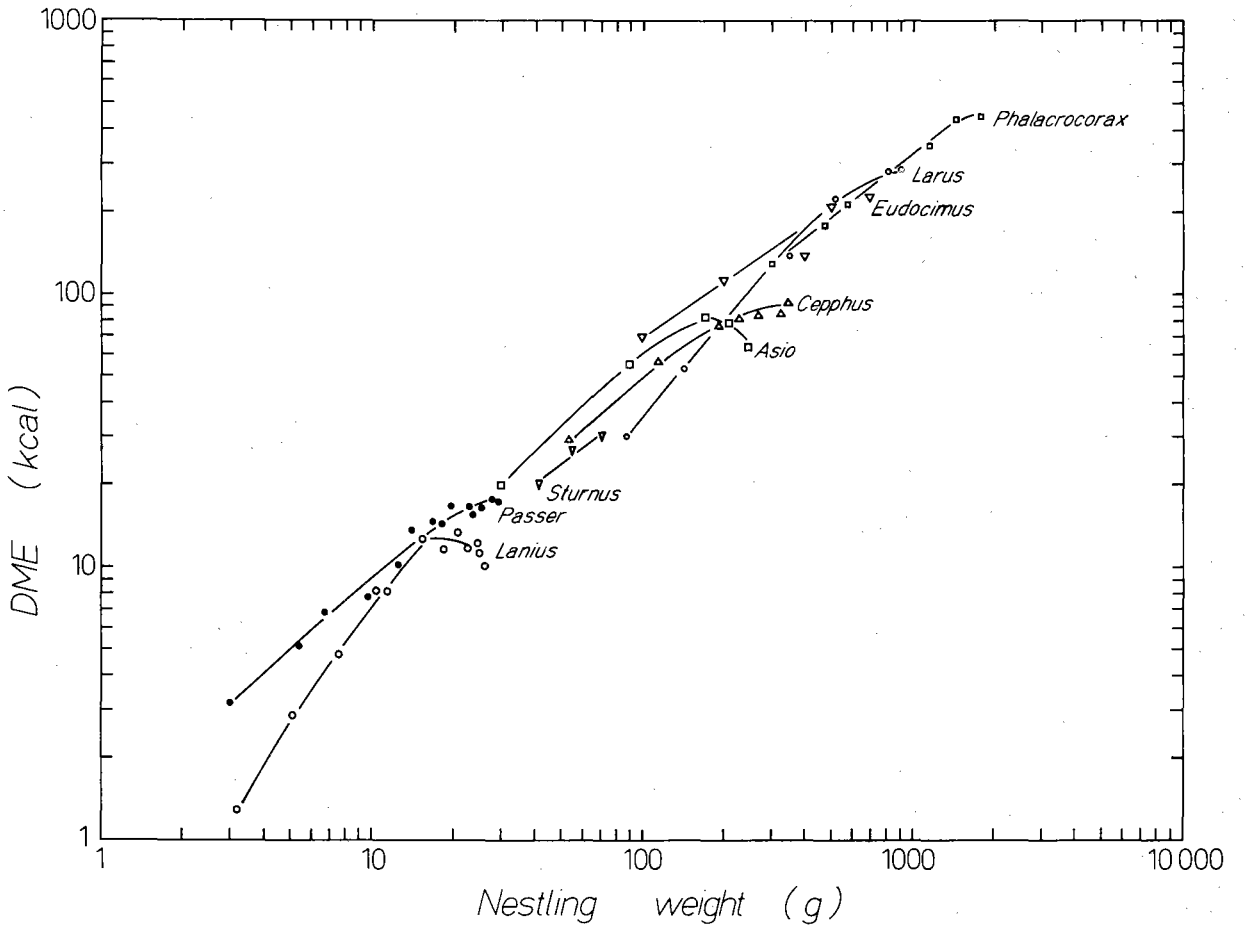


Fig. 9. Daily metabolizable energy (DME, in Kcal per nestling per day) in relation to nestling body weight throughout development in *Passer domesticus* (Blem 1975), *Lanius collurio* (Diehl & Myrcha 1973), *Sturnus vulgaris* (Westerterp 1973), *Asio otus* (Wijnandts, in prep.), *Cepphus columba* (Koelink 1972), *Larus glaucescens* (Drent & Henderson, in prep.), *Eudocimus albus* (Kushlan 1977) and *Phalacrocorax auritus* (Dunn 1975a, 1975b).

of stability of body weight). The distinction is essential if one wishes to consider efficiency of growth, but the parent is not troubled by this theoretical consideration and must provide for both growth and maintenance.

We must turn now to Ricklefs' (1969) growth model, and consider why his conclusion that changes in growth rate would scarcely affect energy requirement (a doubling of growth rate entailing merely 10% increment in energy income) departs so widely from the contention implied in our Fig. 10. The operational partitioning of energy expenditure in growing birds is as follows (Blem 1975, 1978; Dunn 1979; Westerterp 1973). DME = tissue gain (P) + total heat production (MR) + activity costs. Tissue gain is here defined as the increment in caloric content as the bird grows, and does not include the cost of biosynthesis which is part of the metabolic expenditure (MR, sometimes further compartmented into resting metabolism and cost of temperature regulation). Regression analysis of differences in growth rates of individual animals in balance trials has yielded estimates approximating a 75% efficiency in building body fat, and a similar figure (62—80%) for synthesis of protein (Kielanowski 1965).

Basically Ricklefs' (1969, 1976) growth cost model amounts to equating the energy cost (E) to the sum of (increment in weight) x (caloric value)

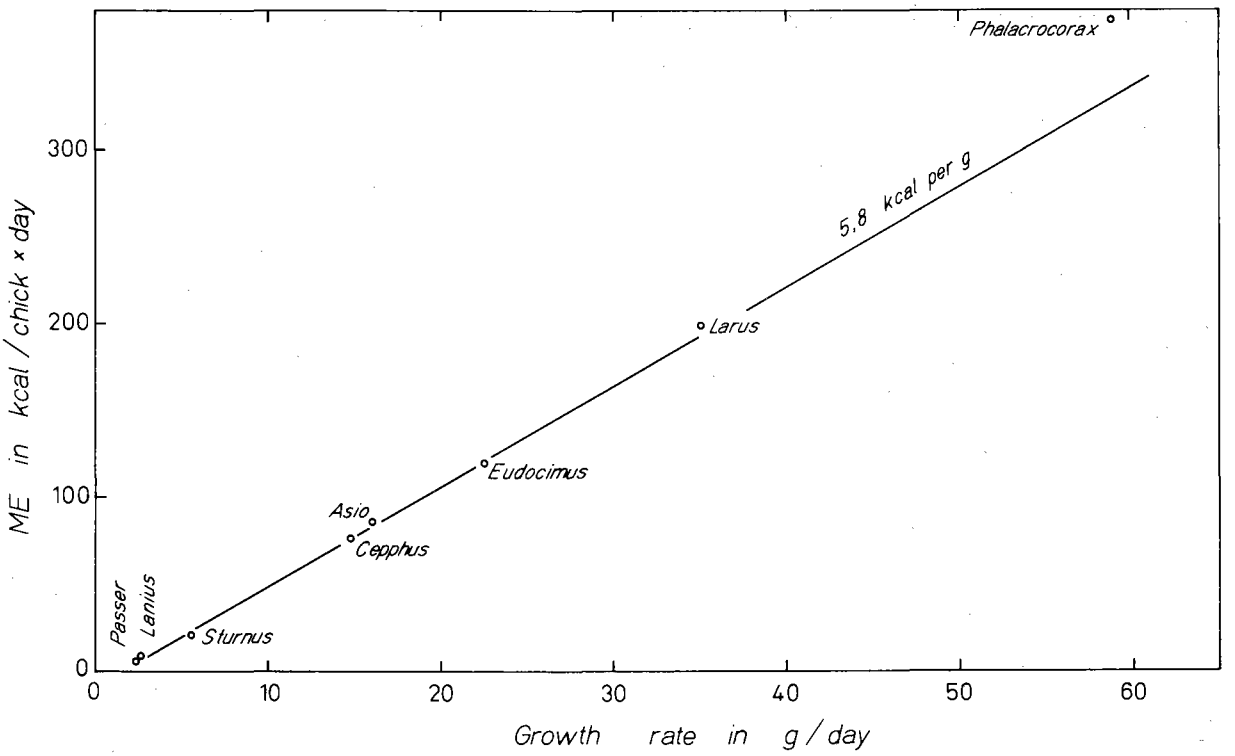


Fig. 10. Energy expenditure of the nestling (DME = metabolizable energy in kcal per chick per day) at the midpoint of the linear growth period, in relation to growth rate achieved at that time, for the species considered in Fig. 9. A one gram difference in growth rate (fresh weight) per day corresponds with a difference of 5.8 kcal in energy expenditure.

and metabolism. By substituting values for resting metabolism, ignoring activity, and assuming caloric value a constant throughout growth (an assumption at variance with the available measurements), Ricklefs was able to estimate energy increments incurred in changing growth rates. Clearly, these estimates depend heavily on the extent to which biosynthetic cost is adequately covered by the resting metabolism values taken, and do not represent an independent approach to the problem of growth cost. Ricklefs himself does not seem to give much credance to his model, since testable predictions derived from it disagree with the facts. In particular the prediction that birds will always sacrifice family size to reduce developmental period and therefore will raise a single young at a rate limited only by the parents' capacity to satisfy the energy and nutrient demands of the growing chick, is belied by the prevalent characteristic of laying more than one egg per clutch, and is at variance with the demonstrated variability of growth rate in singleton broods.

Aside from varying absolute growth rate, the growing chick has the option of reducing the cost per gram of body increment. Fat, often deposited in nestling birds, is not only a reserve intended to ease the gradual transition to self-feeding following nest departure, but is also of significance in bridging gaps in parental food delivery occasioned by vagaries in the food supply. This is clearly indicated in studies of seabirds where the parents must range far during foraging flight, over a notoriously patchy sea, and in hunters of the aerial plankton, swallows and swifts (Koskimies 1950, Bryant 1979). In accord with this principle, Mertens (1977) showed that the Great Tit economised in suboptimal habitat by temporising the deposition of fat depots in the growing young, reducing the commitment per nestling by 5 per cent (considered from hatching to fledging). To illustrate this point, Fig. 11 (constructed from

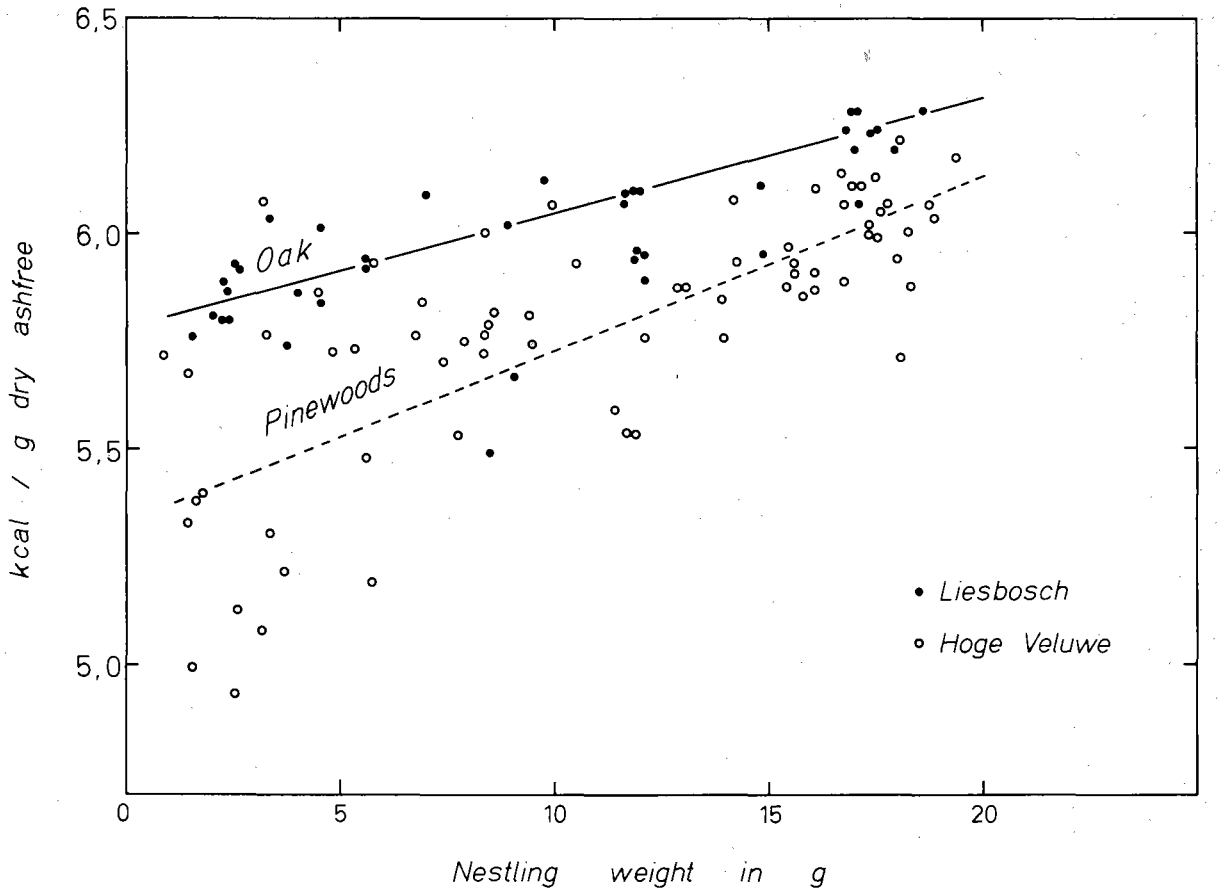


Fig. 11. Economising in growth in the Great Tit: habitat-related differences in body composition of the nestlings (kcal per g ash-free dry weight) in relation to nestling growth (abscissa, nestling body weight in g fresh). At a given body weight caloric content of the oak wood nestlings (Liesbosch) is higher than that in pinewoods (Hoge Veluwe). From Mertens (1978 and personal communication).

Mertens' original analyses) shows the different courses of caloric value of Great Tit nestlings raised in the two habitats (Oak woods = optimal, Pinewoods = marginal). Similar arguments doubtless apply to much of the intraspecific variability in the time course of body weight, and where food supply for the parents has been measured overall growth rates are found to correlate well with indices of food availability (Great Tit, van Balen 1973; House Martin, Bryant 1975, 1979).

## 5. PARENTAL EFFORT AND OPTIMAL WORKING CAPACITY (OWC)

Traditionally the period of nestling care is viewed as a bottleneck in the reproductive cycle, no doubt because the frequent feeding visits to the nest make the idea of parental effort tangible to the observer. As Royama (1966b) pointed out, we lack critical observations for the period immediately after nest departure, and cannot rule out the possibility that this is a veritable "period of crisis". Smith (1978) compared feeding rates of Song Sparrow *Melospiza melodia* broods out of the nest with rates in the foregoing nestling period, and concluded that the interpretation of heightened parental effort in the period of fledgling care fits the facts. Most observations have been done on nestling birds, however, and we shall restrict ourselves to this period.

The problem requiring explanation is that as

brood-size increases, the parents respond by bringing more food, but as revealed by comparisons of nestling weights, the increase is not in proportion to the number of young: nestlings in large broods tend to be undernourished (Perrins 1965, Lack 1966). In the Pied Flycatcher *Ficedula hypoleuca*, von Haartman (1954) studied this relation systematically by adding young to certain broods, thus increasing the range of brood-sizes up to ten (in his Finnish study area the modal brood size was six, the vast majority 5—7, eight rare and larger broods unrecorded). By observation of feeding frequency (supplemented in some instances by measurement of the meal-size by capturing the incoming parent), removal rate of faecal pellets, and growth rates, von Haartman found that contrary to expectation growth in the modal brood was not maximal. Instead, nestling weight showed a gradual decline from broods of two onwards. This finding led him to postulate that the feeding rate for each brood was a compromise between demands of the young and the effort required of the parents to collect the food, and he introduced the concept of "maximal parental effort" (Höchstleistung) to explain how the individual parent reached this compromise. Royama (1966b) took this problem a step further by including implications for mortality, and defined an "Optimal Working Capacity" (OWC) as that working capacity of the parents beyond which they themselves will suffer increasingly from any kind of risks or dangers (*e.g.* physical fatigue, predation, etc.) with the consequence that the number of young they can rear in their life is likely to be reduced. The level of OWC will be far lower than the maximum physical output they can achieve for a short period. Inclusion of lifetime reproductive performance sets an unequivocal target, and the unresolved problem is to determine how the individual parent decides how far to go in any given situation. We will argue that the working capacity of the parents is limited in proximate fashion by physiological constraints defining a sustained work level in metabolic terms. In some situations parent birds may ignore this physiological warning level, but the penalty will be a loss of condition which will in turn entail increased mortality. At this point much of the evidence is circumstantial, but we will develop our point of view by presenting time-budget data for Starling *Sturnus vulgaris* parents feeding young in the nest, obtained by Tinbergen and his collaborators on Schiermonnikoog.

By manning an observation tower overlooking the study colony throughout the daylight hours it was possible to obtain virtually complete time-budget data for the female, and simultaneously all the feedings of both parents were recorded by an automatic camera unit mounted at the back of the nestbox. The nestbox was fitted with an inner box containing the nestlings, mounted on an electronic balance. Hence it was possible for an additional observer to read off total nest weight from a hide behind the nest. On various occasions through the day it was thus possible to obtain body weight of the parents. For the present discussion we will restrict ourselves to weights obtained for the female parent when she remained in the nest following a feeding visit for a sufficiently long period to allow nest weight to stabilize, and departed without removing faecal material. The observation series for 28 May through 3 June 1979 is depicted in Fig. 12, and shows what happened when the number of young in the nest (originally five) was altered (increased to nine on three days, and reduced to two on two days, with two days at the original brood-size for comparison). The series started when the nestlings were 5 days old, and hence all observations stem from the period when normally feeding rate was at a constant level (see Fig. 7). The parents altered their feeding rate according to the brood size, and the correspondence in total number of feedings for the day for a given brood size when the experiment was repeated is striking. In keeping with the results from other studies this adjustment was not proportional to the change in brood size. Daily growth increments for the two nestlings remaining in the nestbox throughout the observation period accordingly lag behind on two of the three days when the parents were confronted with nine young (maximal natural brood size in this area is six). What work level did the female parent achieve on these peak days, when apparently the young were not adequately provisioned? Flight, metabolically the most expensive activity, showed a clear relationship to brood size (see Fig. 12, where flight is entered as per cent of

the daylight hours devoted to this activity). Repercussions to the parent are evident if the body weight is related to flight time. This is shown in Fig. 13 for afternoon weights, as this was the only time of day for which observations were available for all experiments. These data suggest that a daily commitment of more than three hours devoted to flight cannot be met without a decline in body condition. By the steep fall in body weight an asymptotic function is suggested with a value in the neighbourhood of four flight hours as plateau. Data for two other female parents under stress in the nestling period also show maximum commitment in the range of 3—3.5 hours. Hen 34 was paired with a bigamous male who devoted practically all of his foraging time to his other mate, leaving 34 to cope almost single-handed with five nestlings (which fledged successfully).

The mean value for her flight-time per day, averaged over 3 days was 3.05 hours. Hen K suffered from a different handicap. In this case the mate cooperated, but the nestbox was located out on the merse, where intake rates of foraging starlings are markedly lower than in the pastureland surrounding the principal study colony considered so far (Tinbergen 1976, 1980). Extensive observations were therefore undertaken to decide whether the time devoted to foraging, or the time and energy demand for transport (flight time) was limiting in the merse situation, and to this end manipulations of brood size were undertaken. The maximum brood which the adults could provision turned out to be five, and the mean flight sum for the female parent, averaged over two days for the brood of nine, was 3.43 hours (21% of the daylight hours).

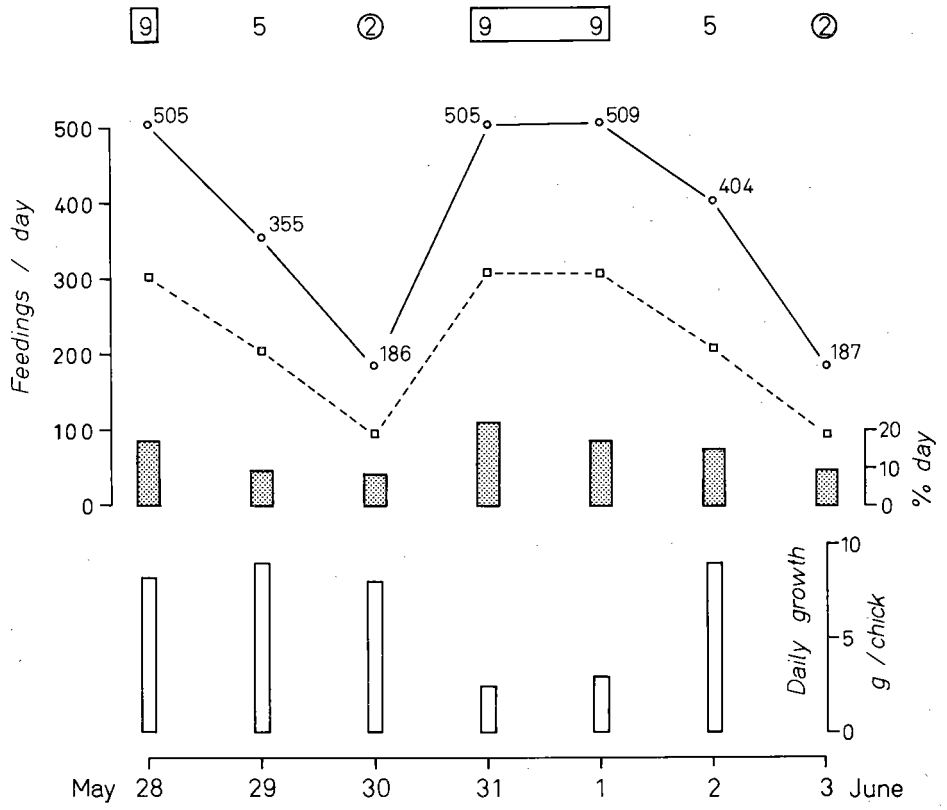


Fig. 12. Response of the parent Starling, *Sturnus vulgaris*, to manipulation of brood size (indicated by numbers along top, 5 being the initial brood size of the pair studied). From top to bottom: feeding rate (solid line total feedings per day, dotted line contribution of hen), flight time expressed as % of active day devoted to flight by the hen (data on male incomplete), and resulting growth in the two individual nestlings present in the nest throughout the experiments (Observations of J. M. Tinbergen and coworkers).

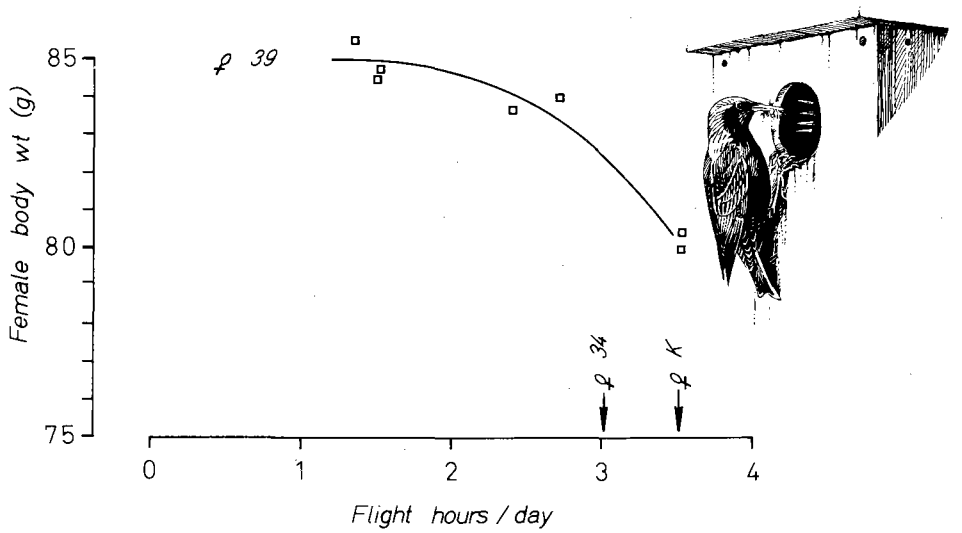


Fig. 13. Repercussions of flight time for body weight in the female Starling when feeding nestlings in the experiments of Fig. 12. The data points show parent body weights taken in the early afternoon in relation to flight time budget for that day (in hours). For comparison the maximum flight commitments of two other hens are shown by arrows (see text; data of J. M. Tinbergen and coworkers).

These starling data suggest the existence of some ceiling for parental performance, in its simplest form an energetic ceiling (see discussion in Drent & Ward, in prep.). Taking the time budget data from the field experiments on enlarged brood sizes and employing energetic equivalents from the literature (fortunately flight cost in this species has been measured by Torre-Bueno & LaRochelle 1978) the female starling appears to operate at a plateau work level of about four times the basal metabolic rate when feeding young (Tinbergen & Meijer, in progress). Some pilot determinations on total daily energy expenditure were undertaken with the aid of the $D_2O^{18}$ technique in 1978 (Westerterp, in prep.) and values for three females provisioning young were obtained, the peak value reaching 3.9 times B.M.R.

Although the level estimated here for the maximum sustained work load is open to question, there can be no doubt that such a limit does exist. The estimation of metabolic level (*i.e.*, the daily metabolizable energy expressed as a multiple of the B.M.R.) typical for parent birds tending broods of the maximum size that can be reared, is a first step to determine if a common energetic ceiling exists. We have arrived at what King (1974) in his critical review terms the current frontier of exploration of time and energy budgets, but where data are few they can be made to fit simple models. The most sophisticated approach to total daily energy expenditure of free-living brids is the use of doubly-labelled water ($D_2O^{18}$), and results are available for two other passerines for the nestling period. Utter & Lefebvre (1973) found two female Purple Martins *Progne subis* to operate at 2.8—3.1 B.M.R. when feeding nestlings (not necessarily at the maximal brood size), a level higher than that of the males which fed the nestlings less consistently. Utter (in King 1974) surmises that 4 B.M.R. is the upper ceiling for reproductive activities, and there are $D_2O^{18}$ determinations for parent House Martins *Delichon urbica*, again females, operating at these levels when confronted with large broods (Bryant & Westerterp, this symposium). Another approach to this problem is to measure energy expenditure of parent birds feeding young in captivity. Dolnik (1972) estimated the maximal sustained effort of Chaffinches, *Fringilla coelebs*, each parent tending ten young, at approximately 3.5 B.M.R. during the waking hours, representing an increment of 31.5 per cent over the cage existence level of the parent alone before

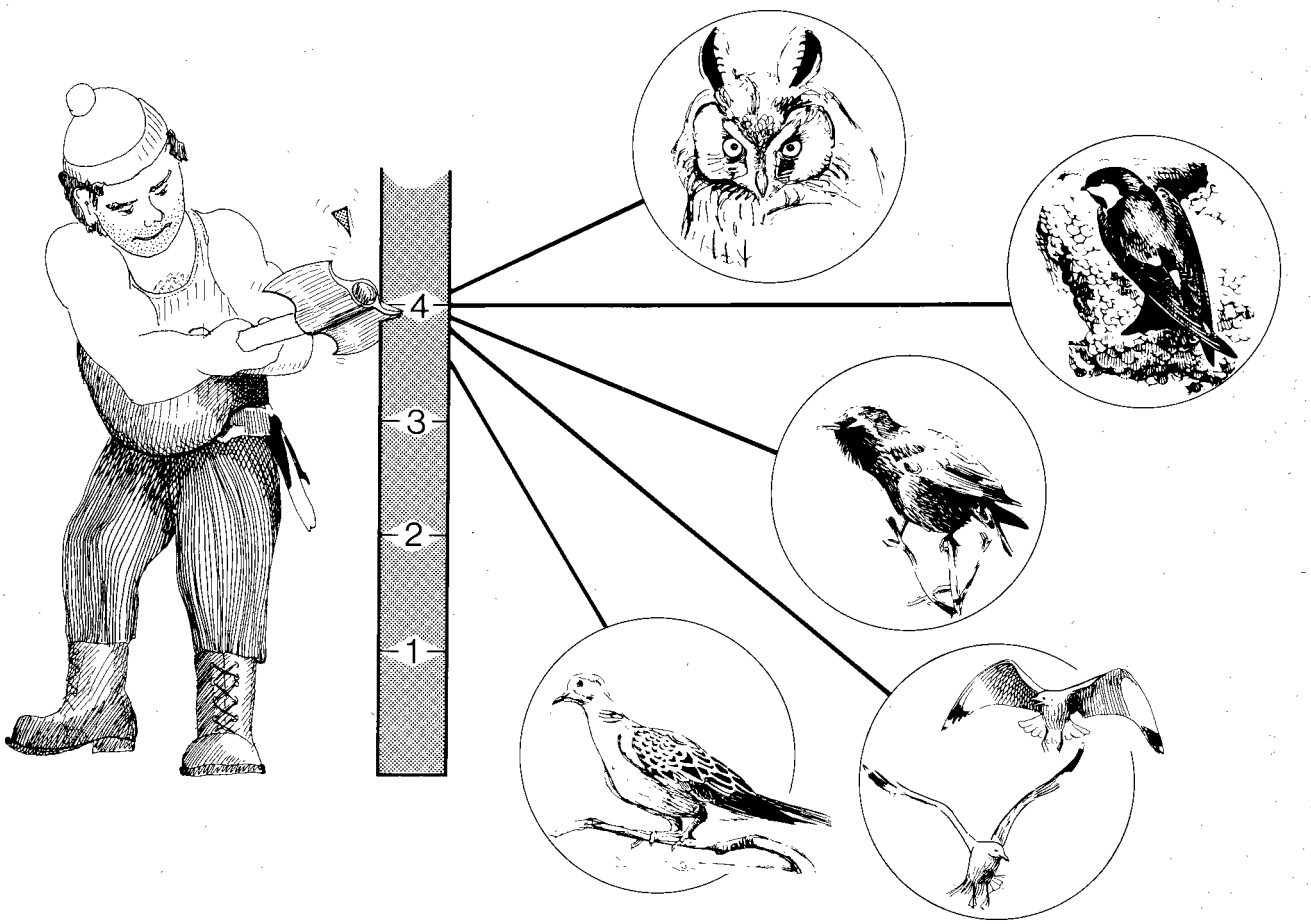


Fig. 14. Maximum sustained working level of parent birds tending nestlings, expressed as metabolizable energy per day (DME) in multiples of BMR (basal metabolic rate). The data refer to *Asio otus* (Wijnandts, in prep.), *Delichon urbica* (Bryant & Westerterp, this symposium), *Sturnus vulgaris* (Westerterp, in progress), *Larus glaucescens* (Drent & Ward, in prep.) and *Streptopelia risoria* (Brisbin 1969) and cluster at approximately 4 BMR, the working level of heavy labour by human standards (Brody 1945).

the trial. From food consumption data given by Brisbin (1969), parent Ring Doves *Streptopelia risoria*, operate at approximately 2.6 B.M.R. when raising a single young, and 3.5 B.M.R. when raising twins. It will be recalled that Murton *et al.* (1974) indicated that the related Wood Pigeon *Columba palumbus* cannot profitably raise more than two young (productivity indices for postfledging survival being 0.11, 0.29, and 0.16 for broods of one, two, and three, respectively). In the Long-eared Owl *Asio otus* telemetry in combination with metabolic trials on birds in captivity allow reconstruction of the energy expenditure of the male when provisioning the female and brood (Wijnandts, in prep.). Finally, in the Glaucous-winged Gull *Larus glaucescens* a time-budget analysis for parents of supernormal broods indicates an operating level of 3.8 B.M.R., an increment of 40 per cent over the incubation phase (this estimate is based on time budget data with costs for gliding and flapping flight as determined in the Herring Gull in wind-tunnel trials by Baudinette & Schmidt-Nielsen 1974).

These crude estimates (assembled in Fig. 14) do not prove the existence of a maximum sustained working level common to all parent birds, but they hint that this may be so. The present data conform to the simplistic view that parent birds, when feeding the young, are able to in-

crease their working level by 33—50 per cent compared to the non-reproductive level (daily existence energy for non-moulting, non-reproductive birds can be estimated at 2.6 B.M.R., see Drent & Doornbos in prep.). The foraging increment as compared to the level typical for self-feeding cannot be estimated in general terms, as this will depend on the return the parent achieves on the energy expended during foraging. The size of food items, the distance of food sources, time of day, and interactions with conspecifics will all influence harvesting rates in addition to food abundance *per se*. A larger increment is possible if the parent is able to draw on body reserves in the nestling period, and this use of an energy subsidy may be a commonly followed tactic (Hussell 1972, Houston 1976). In our view the convertability of time and energy is the major hurdle in life history theory for the field worker, and we suggest that manipulation of brood-size combined with the monitoring of parental energy expenditure is one of the most promising avenues of exploring this problem.

## 6. PERSPECTIVE

In this review we have been concerned with the problem of how individual parents adjust their reproductive effort in order to maximize fitness. The adjustability of laying date, clutch size, pattern of egg care, and after hatching the level of provisioning and the composition of the diet implies a succession of decisions allowing an adjustment of parental effort to achieve a close fit between parental capacity and environmental opportunity. Although we are far from understanding the pattern in detail, we have argued that energy balance is a good candidate for the substrate of decision. Put in other terms, we believe present techniques make the exploration of the proximate control of avian reproduction a promising avenue of research if we are to gain insight in the information relied on by the birds themselves in reaching their decisions.

Problems concerned with initiating a breeding attempt, and details of timing and the determination of clutch size, have been discussed with an emphasis on the pervasive importance of female body condition. The difficulty here is not in conceptualizing how condition impinges on breeding performance for which good circumstantial evidence exists (see reviews by Korschgen 1977 and Newton 1977), but rather in obtaining meaningful indices of body condition. Most data are restricted to total body weight and there is a great need to design techniques enabling assessment of body reserves without sacrificing the bird. Perhaps small tissue samples from the pectoral muscle will prove adequate to follow changes in the protein bank, and it should be possible to estimate the state of fat reserve from blood samples, but these are problems for the biochemist. Certainly, the pioneering efforts of Ward and his associates deserve following up (Jones & Ward 1976), as changes in protein levels are closely geared to the reproductive cycle. How changes in body protein are linked to changes in environmental food supply is a complex issue. Although the efficiency of protein deposition in growing animals has been determined repeatedly (Kielanowski 1966) the problem of defining the right blend of amino acids in the diet offers the investigator a bleak landscape of exhaustive analyses. Fortunately the problem can be attacked in birds with a restricted diet, so is not hopeless.

The nestling stage offers a number of lines of attack for the ecophysiologist. Energy balance of the nestling as a function of brood size is a high priority item where the integration of laboratory and field studies is getting complete (Royama 1966b, Mertens 1979, Westerterp 1973 and in press, Bryant & Gardiner 1979). In the absence of adequate sampling of the energy content of natural feeds the extensive and mutually consistent field estimates of food consumption by weight in nestling tits (Gibb & Betts 1963, Kluyver 1950, Royama 1966b, van Balen 1973, Eguchi 1979) cannot be reconciled with the data from Great Tit broods raised by their parents in captivity (Mertens 1977) which data in themselves provide a reasonable energy budget. This gap in our knowledge demands attention since experiments indicate that the young through changes in their begging behaviour can elicit changes in the types of prey brought to the nest (Tinbergen & Drent 1980) *i.e.* it is unrealistic to assume invariant caloric (and nutrient) input per

gram of food delivered.

Only superficial descriptions of energy balance for the field situation are available. Energy delivered, energy excreted by the young, and energy incorporated in the body tissues can all readily be measured, but the estimation of heat loss and cost of activity presents difficulties. Nevertheless in nidicolous birds general patterns have emerged and we have drawn attention to the similarity in total metabolic expenditure of nestlings of various species when corrected for differences in weight. In addition, the conversion of metabolizable energy into body material seems to obey general rules, since the proportion incorporated into the nestling body is closely similar in the nidicolous species studied to date:

| | | |
|---|---|---|
| *Mycteria americana* | 19% | (Kahl 1962) |
| *Larus canus* | 25% | (Kahru, in press) |
| *Lanius collurio* | 29% | (Diehl & Myrcha 1973) |
| *Sturnus vulgaris* | 26% | (Westerterp 1973) |
| *Passer montanus* | 22% | (Myrcha *et al.* 1972) |
| *Passer domesticus* | 25% | (Myrcha *et al.* 1972) |
| *Passer domesticus* | 23% | (Blem 1975) |

Although some precocial species fall in this range (23% in Domestic Fowl according to Davidson *et al.* 1968), in others (see Kendeigh *et al.* 1977) a much lower figure has been reported. However, in such studies in captivity it is practically impossible to insure that rearing conditions approximate those offered by the parent birds, especially as concerns microclimate. Further study may hence reveal similar consistency in precocial birds.

The implication of the similarity in conversion ratios is that growth efficiency is broadly similar in the various nidicolous situations, but the cost of biosynthesis itself has so far eluded direct measurement. If we take our analysis of differences in metabolizable energy budgets as a point of departure and consider that the caloric equivalent of 1 gram body weight (wet) is often in the order of 1.5—2 kcal, then the cost of adding 1 gram of tissue (wet weight) to the growing bird is presumably in the order of 5 kcal. This type of analysis of growth efficiency is essential if we are to evaluate the savings to the daily requirement involved in slowing the growth rate.

Our analysis of absolute growth rate showed that, in agreement with the extensive analyses of Ricklefs, growth rate in birds can be closely predicted from the adult body weight. Furthermore, the form of the relationship between absolute growth rate and adult body weight is closely similar to that found in mammals (Millar 1977) in that growth rate in both groups varies approximately as the ¾ power of adult body mass. The difference in intercept apparent when the two groups are compared (mammals showing a lower rate of absolute growth at a given body weight than birds) cannot yet be studied since Millar relied on an indirect approximation of growth rate derived from the total time until weaning. Direct comparison of measured increments in weight and in caloric content is called for to elucidate this point. Once these general patterns have been established it is possible to recognize consistent discepancies from the overall prediction, and in keeping with Lack's contention it was found that retardation in growth occurred in several species of birds with very small broods (generally one). In this way energetic demand can be more finely adjusted than by the integer steps of brood size adjustment, and this finding leads logically to the question of the factors limiting adult foraging capacity.

With the advent of the doubly-labelled water technique it has become possible to estimate total energy expenditure of parent birds actively engaged in feeding their young. In combination with brood size experiments it is now possible to delimit the maximum sustained working level. Supplemented by more indirect estimates of energy expenditure derived from time budget observations, the available data do indeed suggest that a general energetic upper level for sustained work exists. Although it would be premature to conclude that the optimal working level has indeed been defined in metabolic terms, these estimates do open the possibility that parent birds reach their decision on how far to invest in their current brood by monitoring energetic exertion. The implication is that work beyond 4 B.M.R. on a daily basis cannot be sustained without impunity, either because the parent cannot physically keep this up (and hence would be forced to cut back its effort drastically in order to recover)

or because exertion beyond this level is detrimental to parent survival. In any case it appears that the "optimal working capacity" postulated by von Haartman (1954) and Royama (1966b) has an empirical basis approachable with physiological techniques along the lines applied to human subjects at work. A further parallel can be traced with the mammal work reviewed by Millar (1977) in that the increase in female metabolism at the peak of lactation seems to reach similar levels, although it must be said that Millar's arguments are indirect.

Meaningful integration of these energetic hurdles with the annual cycle of environmental events is still beyond our reach. Net available energy, which can be defined as energy obtained daily from the environment in return for a given effort, subtracting the energetic costs, is bound to vary through the year. A number of processes which we have linked with changes in body condition may be influenced directly by trends in net available energy, but much will depend on the predictive value of such trends. It would be extremely interesting to obtain data on the rate of energy return per hour of foraging throughout the year, and by studying the costs involved one could determine whether the birds were aiming at a maximisation of intake, a minimization of cost, or some compromise. In particular, it would be illuminating to have information on the seasonal course of foraging returns (such as illustrated by the hunting success rate of the male kestrels considered in Fig. 4) in a large number of individuals in relation to the major reproductive events, in order to see if the reproductive effort of each pair is indeed adjusted to the current rate of return. A complicating factor is the extent to which parents buffer environmental events by anticipatory deposition of reserves. This is commonly observed prior to laying in females and is also a common tactic during incubation, yielding added flexibility in matching daily demand and daily intake in the nestling phase. Identifying a period of energetic surplus does not "explain" the formation of reserves, but rather demands detailed investigation on why energy-costing processes are not put in motion without delay. Selective experiments involving supplementary food as well as increasing costs by manipulating clutches and broods provide ample scope for years to come.

## 7. SUMMARY


1. Energetics of reproduction in birds is reviewed with the question in mind how the parent adjusts its effort in relation to prevailing environmental conditions in order to maximize the output of young in its lifetime. Emphasis is on proximate controls, rather than ultimate factors measurable in terms of adult survival and recruitment of young.
2. The decision to breed or not to breed is clearly related to body condition of the female, presumably because of the implications this has for survival (see Fig. 1).
3. Laying date and clutch size are likewise under the influence of female condition and can hence be modified by experiments involving supplementary feeding (Fig. 2, 3). Natural variation in these features may often be related to territory quality (Fig. 4).
4. How the bird decides whether or not to commence a second brood is not clear, but in the Great Tit the habitat-related difference in incidence of second broods is functionally understandable when survival probabilities of birds at different times are considered (Fig. 5).
5. A distinction is made between a "capital" and "income" model for translating rates of change of female body condition into appropriate decisions on laying date and clutch size (Fig. 6) and experiments are suggested that discriminate between the two.
6. Lack's view that brood size is in an evolutionary sense adjusted in order to balance food requirement and foraging capacity of the parents is accepted, and growth rates in nidicolous birds are analysed to ascertain if a finer adjustment exists superimposed on the integer steps of brood adjustment. Critical for this analysis are groups of birds where broods of one are common, since only in these circumstances is growth adjustment the only strategy open to the parents. In common with other animals, growth rate is related to mature body size (Fig. 8) but within a category of adult weight clear examples can be found for retardation of growth rate in pelecaniform and charadriiform species with singleton broods.
7. Since daily energy requirement is related to nestling size (Fig. 9) and growth rate (Fig. 10), retardation of growth is explicable as a strategy only in terms of reducing the daily commitment of the parents, not reducing the total cost of producing a nestling.
8. An additional economy in growth is to reduce the contribution of fat to the nestling body (Fig. 11).
9. Implied in Lack's view of brood size is a limitation of parental foraging capacity, and the last section of the paper is devoted to exploration of the proximate factors delimiting what Royama terms the optimal working capacity of parents feeding young. Observations of parent starlings confronted with manipulated brood size suggest a limit on the time that can be devoted to energetically extravagant flight activity, rather than a shortage of absolute time (Fig. 12). Beyond the limit to which stressed parents can be made to fly, body weight declines (Fig. 13).
10. Preliminary data on energy metabolized daily by parents confronted with large broods conforms to the simplified view that parental effort on a sustained basis equates to energy mobilization equivalent to 4 B.M.R. units (Fig. 14)

and it is suggested that this level of energy expenditure represents a proximal decision substrate for determining the optimal working capacity of the parent.

11. The paper ends with a plea for more research on the proximate controls of avian reproduction, and calls attention to the central importance of the protein bank to parental body condition.

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10. APPENDIX. Growth rate in diurnal raptors

| Species | Adult body weight (g) | Daily increase (g) | Locality | Authority |
|---|---|---|---|---|
| *Accipitridae* | | | | |
| Accipiter nisus | 300 | 16.0 | Scotland | Moss 1976 |
| Circus ranivorus | 420 | 28.0 | Africa | Brown & Amadon 1968 |
| Circus cyaneus | 530 | 25.0 | Orkneys | Scharf & Balfour 1971 |
| Circus aeruginosus | 760 | 37.4 | Neth. | Wildschut unpubl. |
| Buteo buteo | 950 | 46 | Germany | Mebs 1964 |
| Buteo lagopus | 1040 | 36.7 | Norway | Hagen 1969 |
| Parabuteo unicinctus | 1090 | 42.9 | Arizona | Mader 1975 |
| Milvus milvus | 1119 | 40 | | Wuttgy in Glutz 1971 |
| Buteo jamaicensis | 1220 | 38.7 | California | Sumner 1929 |
| Buteo jamaicensis | 1220 | 40.6 | California | Fitch et al., 1946 |
| Pandion haliaetus | 1600 | 51.4 | Virginia | Stinson 1977 |
| Haliaetus vocifer | 3400 | 82 | Africa | Brown & Amadon 1968 |
| Aquilo chrysaetos | 4690 | 105 | California | Sumner 1929 |
| Gyps africanus | 5300 | 72.5 | Serengeti | Houston 1976 |
| *Torgos tracheliotus | 7500 | 133 | Serengeti | Pennycuick 1976 |
| *Gyps fulvus | 8200 | 125 | Armenia | Geilikman 1966 |
| *Falconidae* | | | | |
| Falco sparverius | 119 | 7.7 | Oregon | Roest 1957 |
| Falco sparverius | 120 | 7.7 | California | Sumner 1929 |
| Falco tinnunculus | 250 | 13.2 | Neth. | Cavé 1968 |
| Falco columbarius | 538 | 26.9 | California | Fowler in Ricklefs |

* See footnote table 1. Adult body weight refers to females.